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GENETICS

of EASTERN COTTONWOOD

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This publication is one in a series on the genetics of important forest trees of North America published by the Forest Service, U.S. Department of Agriculture, in cooperation with the Society of American Foresters. Development of this series is in accord with the resolutions of the World Consultation on Forest Genetics and Tree Improvement at Stockholm in 1963 and by the Fifth World Forestry Congress in Seattle, 1960. The Committee on Forest Tree Improvement of the Society of American Foresters undertook the preparation of manuscripts for North American species.

SUMMARY ABSTRACT

There is an increasingly urgent need for higher production of quality wood on short rotations for reconstituted wood products, veneer logs, and sawtimber. This will require trees with inherently rapid growth to justify much more intensive culture than has been economically feasible in the past. Hybrid poplars can best meet these requirements for very short rotations: 2 to 8 years for fiber or reconstituted wood products, and 15 to 25 years for veneer or lumber. Although all crossable species of *Populus* should be used for ultimate maximum genetic improvement of the genus, this paper is limited to the use of *P. deltoides* (eastern cottonwood) as the basic species for development of improved multiclonal varieties.

The major objectives for genetic improvement should be maximum production of wood for specific uses on the shortest possible rotations, wide environmental adaptability, and pest resistance. The seed-orchard approach will not produce the maximum or earliest improvement in forest trees, such as poplars, for which economically feasible methods for clonal propagation of commercial planting stock are (or become) available.

Because clonal propagation permits the immediate multiplication and use of genetically superior individuals without dilution or adulteration of the genotypes, earliest and maximum improvement in poplars will be through multiclonal varieties. Hybrid clones in such varieties can be replaced when they begin to lose their value because of a change in industrial use requirements, increasing disease or insect susceptibility, or decline of general fitness resulting from long-term climatic changes.

Breeding to obtain multiclonal varieties should follow the same general methods as for the development of varieties to be propagated by seed including intraspecific pedigree breeding, species hybridization, controlled sib- and back-crosses, and some kind of recurrent selection. Polyploidy will also have value.

Gene pools of both native and exotic poplar species should be established at all centers of poplar improvement to provide the broadest possible genetic base. This objective will require the conservation of both identifiable and cryptic variation. Clonal tests and the progenies derived from breeding can serve also as gene pools for pedigree breeding and mass selection.

Genetic improvement of *P. deltoides* may be accomplished through:

(1) plus-tree clonal propagation and evaluation;
(2) half-sib propagation and evaluation;
(3) intraspecific breeding; and
(4) species hybridization.

The first step for the genetic improvement of eastern cottonwood should be the selection of plus trees from throughout the natural range for clonal tests and for the establishment of gene pools.

Selection and clonal testing of plus trees is the simplest improvement procedure and can begin to provide material for commercial planting within 3 to 4 years. There would be relatively little risk in using 25 to 50 local plus-tree clones in multiclonal varieties before field tests have indicated the superior clones.

The dual objective for evaluation and propagation of half-sibs from plus trees would be (1) clonal field tests of ortets selected on the basis of nursery screening, and (2) establishment of combination "gene pool-progeny test" plantations, primarily to provide gene pools for future clonal selection and breeding, but also to obtain some information on heritability.

Species hybridization will provide the maximum genetic diversity. Hybridization may begin as soon as pollen and female flowering branches are available, or it may be delayed until nursery evaluation has provided at least preliminary information on nursery performance of the plus trees and on the general combining ability of the female plus trees included in the half-sib tests. All available poplar species should be used for hybridization with *P. deltoides*.

GENETICS OF EASTERN COTTONWOOD

by Ernst J. Schreiner[1]

INTRODUCTION*

Economic trends in forestry indicate the need for high production of quality wood on short rotations, not only for fiber or chemical use (reconstituted wood products) but also for veneer and sawtimber. This will require trees with sufficiently rapid growth rates to justify much more intensive culture than has been economically feasible in the past.

Synethetic multiclonal hybrid variety of poplar can be created to meet these requirements for extremely short rotations (2 to 8 years) for fiber or chemical uses, and for 15- to 25-year rotations for veneer or lumber (depending upon length of the growing season, growth potential of the site, and intensity of culture). A synthetic multiclonal hybrid variety would be a *mixture of adequately tested hybrid clones* representing a diversity of parentages but sufficiently similar in their growth requirements to be grown in random mixture (Schreiner, 1966a, 1966b, 1967).

Natural poplar hybrids have been used in European poplar culture for at least 150 years. But Augustine Henry, professor of forestry at the Royal College of Science, Dublin, was probably the first to report the artificial production of poplar hybrids (Henry, 1914).

Although the urge to hybridize forest trees was at least 100 years old, Easter Monday, 21 April 1924, marked the birthday of what was apparently the first large-scale breeding project in the world devoted exclusively to the genetic improvement of forest trees (Schreiner, 1950). The objective was to produce rapid-growing poplar hybrids for pulpwood reforestation (Stout, *et al.*, 1927). Since 1924, and particularly since the end of World War II, there has been a world-wide boom in work on the genetic improvement of poplars.

Poplar-improvement projects are too numerous and too diverse to permit adequate summarization in this report. In many countries current projects include basic genetics research, breeding, and extensive clonal testing of both natural and artifically produced hybrids. In the United States the Southern Hardwoods Laboratory of the USDA Forest Service is engaged in a comprehensive research project on the improvement of *P. deltoides* in the lower Mississippi Valley (Farmer, 1966b).

Our American *Populus deltoides, P. tremuloides,* and *P. trichocarpa,* three of the best timber poplars in the world, merit genetical improvement through selection and hybridization. Although all crossable species of *Populus* should be used for ultimate maximum genetic improvement, this paper will be limited to the use of *P. deltoides* as the basic species for the development of improved synthetic multiclonal varieties. The creation of such synthetic varieties for commercial use throughout and beyond the botanical range and native habitats of *P. deltoides* will require cooperation on plus-tree selection and clonal testing (and if possible on breeding) among poplar projects throughout the United States and southern Canada.

Taxonomy

Native poplar species.—The five sections recognized in the taxonomic classification of *Populus* and the species native to the United States are:

Section POPULUS[2] (LEUCE Duby) (WHITE POPLARS, ASPENS)—*P. tremuloides* Michx., *P. grandidentata* Michx.

Section LEUCOIDES Spach—*P. heterophylla* L.

Section TACAMAHACA Spach (BALSM POPLARS)—*P. angustifolia* James, *P. balsamifera* L., *P. trichocarpa* Hook.

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* Information presented in this paper was current as of January 1969.

[2] International Code of Botanical Nomenclature Article 22 in 1966 edition).

Section AIGEIROS Duby (COTTONWOODS, BLACK POPLARS)—*P. deltoides* Bartr. var. *deltoides, P. deltoides* var. *occidentalis* Rydb., *P. fremontii* S. Wats, var. *fremontii, P. fremontii* var. *wislizeni* S. Wats.

Section TURANGA Bge.—No native species.

Native AIGEIROS poplars.—The nomenclature of the American cottonwoods is slightly confused. The currently accepted Forest Service nomenclature is listed below; because Rehder's "Manual" is widely used, his species are listed as synonyms:

*Accepted nomenclature**	*Synonyms***
P. deltoides Bartr. var. *deltoides* (fig. 1)	*P. deltoides* Marsh. *P. angulata* Ait. *P. palmeri* Sarg.
P. deltoides var. *occidentalis* Rydb. (fig. 2)	*P. sargentii* Dode *P. texana* Sarg.
P. fremontii S. Wats. var. *fremontii* (fig. 3)	*P. fremontii* S. Wats *P. macdougalii* Rose
P. fremontii var. *wislizeni* S. Wats. (fig. 3)	*P. wislizeni* (S. Wats.) Sarg. *P. arizonica* Sarg.

The taxonomic confusion is understandable because the range, particularly of *P. deltoides* (figs. 1 and 2), is extensive and because the more or less linear natural distribution on bottomlands of the major rivers and their tributaries presents innumerable geographic barriers to free and easy gene flow. There is evidence for long-distance dissemination of poplar pollen and seed. My observations during 44 years have indicated that in the Northeastern Region *deltoides* can become established in the uplands on disturbed sites, such as gravel and sand pits, in years when there is sufficient moisture to permit seed germination and survival. Nevertheless, gene migration from one major river valley to another is probably a relatively slow process.

Natural hybridization and introgression with other native species of poplars has further complicated the taxonomic treatment of the cottonwoods. In the Northeastern Region there are several locations where the cottonwood has produced putative hybrid swarms with *Populus balsamifera, P. tremuloides,* and *P. grandidentata.* Brayshaw (1966) has reported putative natural hybrids involving ***P. balsamifera, P. trichocarpa, P. tremuloides,*** and ***P. deltoides*** var. *occidentalis* in southern Alberta.

Another reason for the taxonomic confusion has been the wide variety of clonal material available in arboretums, botanical gardens, and amenity plantings. Many taxonomists have failed either to recognize this fact or to appreciate the taxonomic variability among clones of the natural species.

Silvics

Williamson (1913) presented an exceptionally complete and accurate account of the silvics and management of cottonwood, including the management of natural stands, nursery production of seedlings, the use of seedlings and cuttings in plantations, site requirements, site preparation, spacing, and plantation culture. Most of the work on these aspects since 1913 has in essence merely confirmed Williamson's observations and recommendations; witness these citations from Williamson:

> The fact that this species is seldom found growing naturally far from streams or moist bottom lands is the result of the failure of its seed to germinate satisfactorily on any but moist exposed mineral soils, such as are provided by the deposits from spring floods. This difficulty, however, is avoided by planting young trees. When the roots of the planted stock penetrate to a moist subsoil the tree displays its usual rapid development. (p. 48).
>
> Moderately well-drained, permeable bottom lands afford the best planting sites. The soil need not be rich or loamy. Very sandy land will be sultable if the water table is within from 12 to 15 feet of the surface. Even upland sites may sometimes be suitable provided the soil is not too shallow and rainfall is abundant and well distributed. Suitable upland sites, however, are apt to be well adapted for farming (p. 49).
>
> Planting without a thorough preparation of the site is inadvisable. On freshly cut-over land the preparation should be practically

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* Accepted for USDA Forest Service publications; personal communication from Elbert L. Little, Jr.

** Rehder (1940).

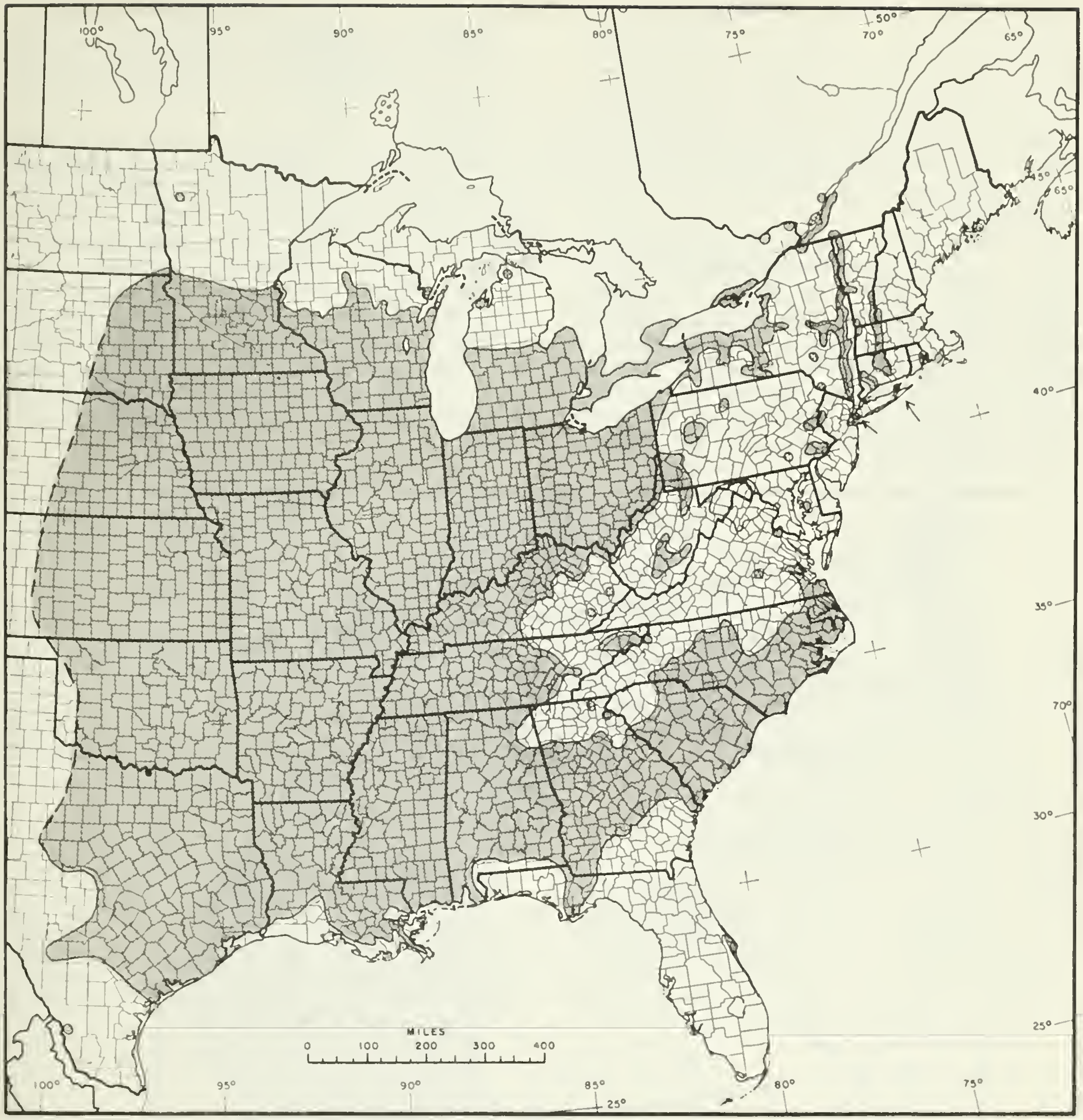

Figure 1.—The range of *Populus deltoides* Bartr. var. *deltoides*.

the same as for natural reproduction. Full sunlight is equally indispensable both for natural grown and planted cottonwood. Planting on heavy sod is never advisable. If plantations are to be established on improved farm land for windbreaks, it will be of advantage to plow and harrow the ground. (pp. 51–52).

Habitat.—The AIGEIROS poplars are generally considered bottom-land species, and relatively few foresters in the past have dared to try or to recommend commercial poplar culture on upland sites. The natural distribution of these poplars along river courses in Europe and America may have been responsible for this traditional notion that for timber production they are adapted exclusively to bottom-land sites. This is true for natural regeneration by seed.

Bare soil, free from sod and weed growth, and continuous moisture at the soil surface for several weeks at the time of seed germination are essential for seed germination and seedling survival. Such conditions are most frequent on river-bottom lands that are subject to periodic overflow; they are too infrequent on upland sites to bring the poplars out of the river valleys by natural seeding.

But the culture of genetically superior poplars is not based on the uncertainty of seed reproduction (direct seeding). Plantations could be established with superior seedling stock; genetically superior clones must be established with dormant or rooted cuttings. There are many upland sites where soil depth, texture, fertility, pH, and available soil moisture during the growing season are sufficient for excellent growth of fast-growing poplars. And there are bottom-land soils of low fertility, low pH, or inadequate aeration where the poplars grow as poorly as on infertile or dry upland soils.

Plantation establishment.—Rapid-growing poplars cannot be successfully established on abandoned fields or brush land without site preparation (Williamson, 1913; Schreiner, 1937). Because the root and shoot growth of cottonwood is considerably retarded when sandy loam soil is compacted to a bulk density of 1.60, old-field and other compacted soils should be deep-plowed well in advance of planting (Broadfoot and Bonner, 1966). Plantations must be kept free of grass and weeds for at least the first year after planting (Schreiner, 1945).

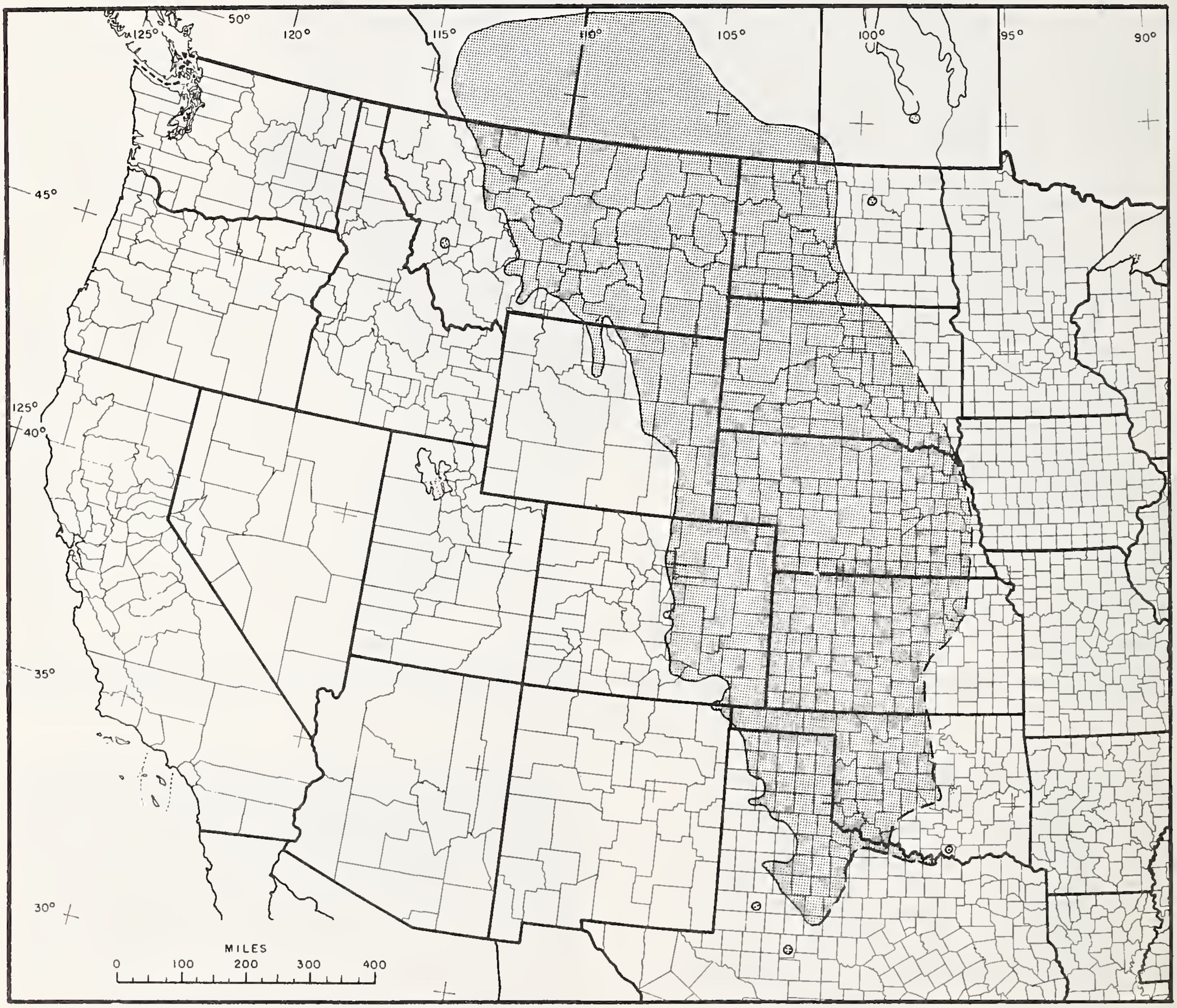

Figure 2.—The range of *Populus deltoides* var. *occidentalis Rydb.*

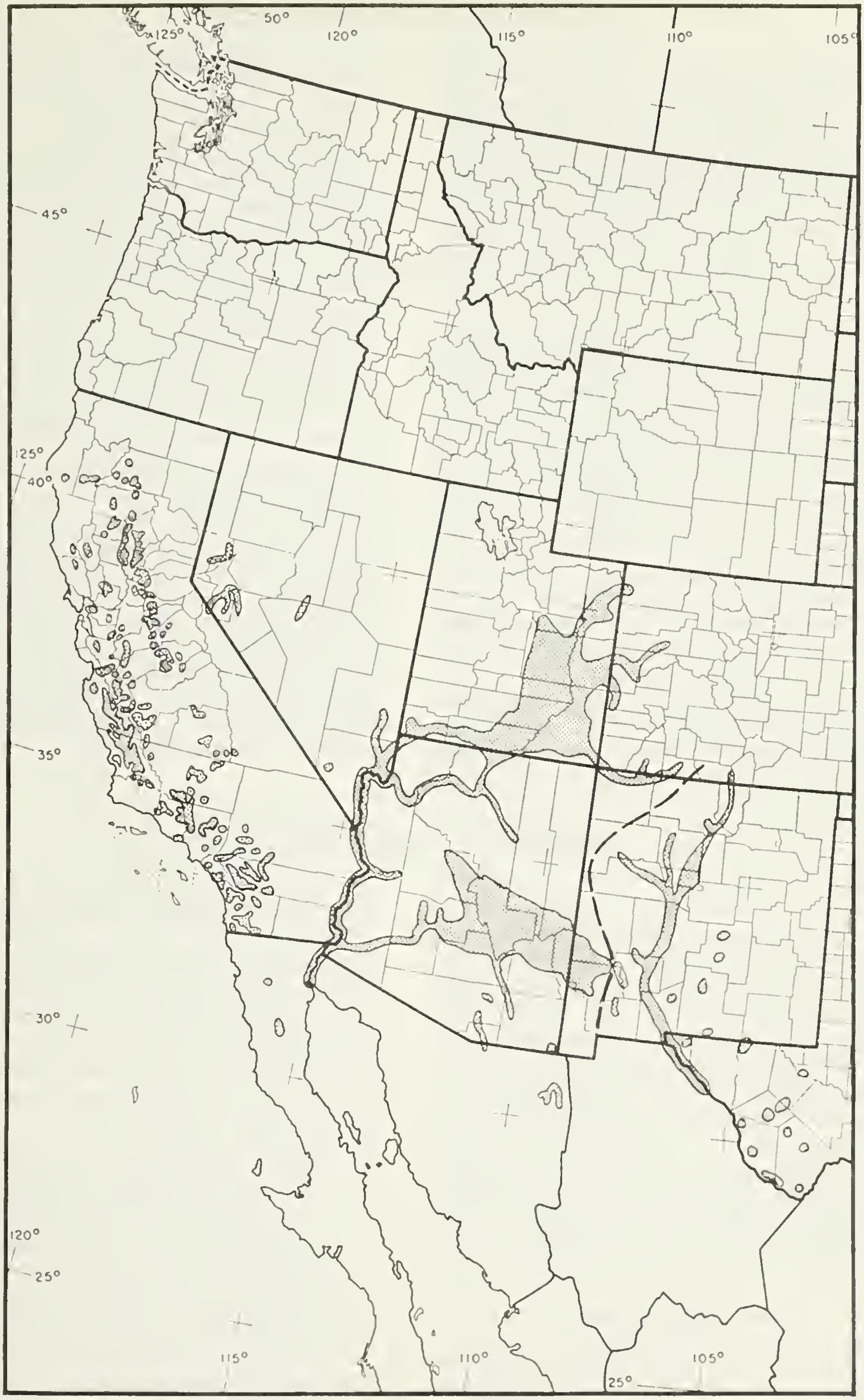

Figure 3.—The range of *Populus fremontii* S. Wats. Broken line separates var. *fremontii* (west) and var. *wislizeni* S. Wats. (east).

SEXUAL REPRODUCTION

All poplar species have been classified by Rehder as dioecious; but *P. lasiocarpa* Oliv., introduced from China into the United States in 1904 (Rehder, 1940), has been described as a poorly known monoecious, self-fertilizing species (FAO, 1958). Deviations from strict dioecism have been found in individual trees of POPULUS (LEUCE), AIGEIROS and TACAMAHACA poplars (Lester, 1963; Melchior, 1967; Avanzo, 1967).

Populus deltoides begins to flower when the trees are 10 to 15 years old, but the flowering age of individual trees of *P. deltoides* and also of hybrid poplars varies considerably. In forest plantations in western Maine trees of *P. deltoides* began to bloom between the tenth and fifteenth years; the flowering age for individual hybrids varied from 8 to 15 years. In western Massachusetts a very few hybrids began to flower at 6 years, but the majority of the clones came into bloom between 8 and 15 years.

The sex ratio, based on 551 flowering trees in the lower Mississippi Valley, was 54 percent males and 46 percent females. Males were slightly but insignificantly larger in diameter and significantly taller than females but there was no relationship between sex and form class, stem straightness, branchiness, or specific gravity of the wood (Farmer, 1964).

There is wide variation in the time of flowering and fruiting of *P. deltoides* throughout its extensive range; anthesis occurs from early March to late June and seed maturation from May to late August. In the lower Mississippi Valley the differences in flowering time among trees within stands are also significant (Farmer, 1966a).

Male and female flowers can be forced, as needed, over a period of at least 1 month on flowering branches held in cold storage. Pollen can be kept viable by storage over calcium chloride at room temperature for at least 1 to 2 weeks, and somewhat longer at 25 percent humidity at 1° to 4° C.

Individual trees normally produce fair to heavy seed crops every year. A bushel of fresh catkins yields about 2 pounds of seed, and the cleaned seed averages about 350,000 seeds per pound (Fowells, 1965). At the time of this writing, 1968 *P. deltoides* seed stored in stoppered vials in a household refrigerator at approximately 1° to 4° C. for 6 months is still 100 percent viable; *P. alba* seed stored 18 months gave 60 percent germination.

GENETIC IMPROVEMENT

The overall objective should be the maximum production of wood for specific uses on the shortest possible rotations. This will require breeding for the improvement of both forest requirements and use requirements. In this paper, *requirement* is used in one of its most common meanings: "that which is needed . . . a required quality." *Forest requirements* are those characteristics and qualities of the tree that are essential for its successful culture, such as rapid growth, climatic and site adaptability, and pest resistance. *Use requirements* are the characteristics and qualities of the tree that determine its value for special uses.

Forest Requirements

Growth rate.—The increasing economic pressure for intensive forest culture will make rapid growth a *sine qua non* for profitable poplar culture. Breeding for wide environmental adaptability will be essential because of the inevitable correlation between growth rate and environment.

Evidence for ecotypic and individual variation of the photoperiodic response in *P. deltoides, P. trichocarpa* and *P. balsamifera* has been presented by Pauley and Perry (1954) and in *P. deltoides* and *P. tremuloides* by Vaartaja (1960). With reference to breeding, Pauley and Perry (1954) note:

> Because of its fundamental role in the vegetative growth cycle, the photoperiodic response should obviously be a matter of primary concern to the tree breeder. As a means of increasing the net yields of wood or fiber, gene combinations nicely adapted for full utilization of the growing season in a particular habitat, may well prove to be quite as promising as a search for heterotic hybrids.

Range-wide provenance tests of the American cottonwoods are needed; such tests can be combined with the gene pools discussed later in this report.

Poplar clones can vary widely in their growth response to the nutritional environment. Curlin (1967) reported a strong clone x nitrogen fertilizer interaction for diameter, height, and volume growth among 22 clones of *P. deltoides*, and cautioned that it would be unwise to select eastern cottonwood from a nutritional environment other than the one in which it ultimately will be grown. "Frequently a clone which performed poorly under unfertilized conditions excelled when fertilized and in several instances the reverse was true."

Pest resistance.—If poplars are not the most pest-ridden of the world's important timber trees, they certainly rank high in this respect; but few genera of timber trees, if any, offer better possibilities for rapid genetic improvement in pest resistance (Schreiner, 1963). Pest-resistance improvement will require consideration of the effect of environment on the resistance or susceptibility of the host, on the biology and pathogenicity of the pest, and on the host-pest relationship (Donaubauer, 1966; Schreiner, 1960, 1966a).

Diseases.—At least 10 diseases, including a virus, are now considered of major importance (and at least 15 are of minor importance) on poplar species and hybrids that may be used for genetic improvement of *P. deltoides*. The virulence of most of these diseases depends upon the effect of the environment on the growth-vigor of the host. Therefore improvement in adaptability to inimical environmental conditions must be considered in breeding and testing for resistance to poplar diseases.

Insects.—On the basis of present knowledge, improvement in insect resistance probably will be more difficult than improvement in disease resistance. Maisenhelder (1960) listed the cottonwood twig borer, the cottonwood root and stem borer, and the cottonwood leaf beetle as the three most serious insects on *P. deltoides* in the lower Mississippi Valley and included seven other insects among those of minor importance. Craighead (1950) listed more than a hundred insects on poplar species in the Eastern United States, at least a dozen of these could become of major importance in commercial plantations.

Twenty-six insects of major or minor importance have been reported in European poplar plantations; some of these are also found in the United States (Schreiner, 1959). Arru (1964–65) has reported massive infestation by the poplar tentmaker, *Pygaera anastomosis* (L), resulting in total defoliation in various localities of northern Italy. He has also identified 12 species of leaf miners on poplars in northern Italy (Arru, 1966–67).

There is evidence for inherent variation in resistance to the Japanese beetle among full-sib hybrid poplar clones (Schreiner, 1949). Cadahia's (1965) report on the presence of a chemical attractant in the host for oviposition by *Sternochetus* (= *Cryptorhyncus*) *lapathi* L. may open the way for a chromatographic approach to identify the host traits responsible for borer resistance.

Nematodes.—Information is insufficient for predicting the probable importance of nematodes in commercial poplar culture. Ruehle (1967) has listed 19 species collected from poplars, but only one (*Meloidogyne* sp.) as associated with plant injury in Israel.

Rodents.—Chiba (1966) has presented evidence for inherent resistance in poplars to injury by mountain hares and field mice in Japan. Resistant clones of *P. maximowiczii* transmitted this character to their hybrids with *P. nigra*, and similar results were obtained in hybrids between white poplars and aspens.

Use Requirements

Unfortunately, many use requirements have not yet been defined with sufficient clarity for use in individual tree selection. For example, relatively few of the requirements for pulp and paper (Schreiner, 1935, 1958) have been related to specific physical and chemical characteristics of the wood.

Timber form.—Selection and breeding of poplars should be for straight concentric stems, narrow crowns with a minimum number of small-diameter branches, and minimum epicormic branching. Selection for natural pruning is unrealistic because the overall objective is to produce quality wood on a short rotation, 15 to 25 years for lumber or veneer. Natural pruning will not produce an appreciable volume of knot-free wood within this short period; artificial pruning will be necessary for such short rotations. There is ample evidence that in poplars the genetic variability in all of these traits, including lack of phototropic response to eliminate trunk lean (Werner and Dagenbach, 1965; Barner, 1965), is sufficient for improvement through breeding and clonal selection.

Wood characteristic and qualities.—For many wood properties the evidence conflicts as to whether they are under sufficient genetic control to make possible the creation of clones with the potentiality to produce the desired qualities under a reasonably wide variety of environmental conditions. There will be need for clonal evaluation of the wood properties that are important for the use of poplar as veneer; sawtimber; and reconstituted wood products such as pulp and paper, particle board of various kinds, and chemical conversion products. An example of such a study is the report by Sachsse (1961) on the Oxford Poplar and two other hybrid clones that are being grown in Europe.

Genetic variation is sufficient among individuals in specific gravity, fiber length, and overall pulp quality to warrant the expectation of genetic improvement for these traits. The specific gravity in a lower Mississippi Valley cottonwood population varied from 0.32 to 0.46 and averaged 0.38 (Farmer and Wilcox, 1966a). The authors note that selection for high-density (or low-density) trees would be possible, but because the correlation between the specific gravity of juvenile and of more recently formed wood was relatively low, selection for specific gravity at an early age may not be efficient.

Boyce and Kaeiser (1961) reported that the mean fiber length (at d.b.h.) among 83 trees of *P. deltoides* varied from 0.85 to 1.28 mm. The number of annual rings and the diameter accounted for at least 50 percent of the variation; the genetic variance was estimated to be about 30 percent. They concluded that the results of their study " . . . can be used to identify trees with fibers inherently longer than the average for natural trees."

Kennedy (1957) found that fast growth does not have a deleterious effect on fiber length in *Populus trichocarpa*. In fact, evidence indicated that the fast-growing trees produced longer fibers; such positive correlation is of considerable importance because rapid growth is the overall objective.

In a study of 13 of the Northeastern Forest Experiment Station's hybrid poplars representing seven different parentages, Hamilton and Wendel (1967) found no significant differences in fiber length among clones. But the average specific gravity for individual clones ranged from 0.29 to 0.38; the average for all clones was 0.33. The ranking by clones indicated four distinct groups that differed significantly from one another but did not differ within a group. The Oxford Poplar, which is being recommended for commercial planting in Europe, had an average specific gravity of 0.38.

A preliminary study based on three ramets of each of three 13- to 14-year-old Northeastern Forest Experiment Station hybrids indicated that pulp quality and increased growth rate are not detrimentally correlated (Marton, *et al.*, 1968):

> In spite of the relatively few trees involved in this study, it was apparent that increased growth rate did not present a detriment to pulp quality. In fact, the faster-growing trees within a clone generally gave the best pulp quality. Since the effect of growth rate was least for wood quality and greatest for pulp quality, the forest manager may be doubly advised to grow selected poplar material at a maximum rate in production plantings.

Use of Natural Hybrids

Early European poplar improvement was based on the selection of natural hybrids, particularly hybrids between the European *Populus nigra* and the introduced *Populus deltoides* (Schreiner, 1959). The possibilities for selection of natural hybrids in the United States are too limited to warrant exploitation because exotic species or hybrids have not been used in commerical plantations. Exotic species have been grown as specimen trees in botanical gardens and arboretums, but only very occasionally as amenity trees.

The Lombardy poplar, a cultivar of *P. nigra* introduced to the United States about 1784, has been widely planted throughout the country. Cultivars of other European hybrids, including 'Serotina' and 'Eugenei', have also been widely distributed by nurserymen under the collective common name of Carolina poplar. Natural hybridization has occurred where exotic species and European cultivars have been planted within pollination range of our native cottonwood, but the survival of such hybrids would depend upon a combination of favorable site conditions that are seldom present where poplars are most generally used as amenity trees. Where promising individuals of such natural hybrids are available, they should be selected as plus trees for clonal tests and used in the breeding program.

IMPROVEMENT PROCEDURES

The genetic improvement of most forest tree species has been directed primarily toward the establishment of plus-tree seed orchards. Unfortunately this approach has overemphasized the concept of "improving a species".

The seed orchard approach will not produce the maximum or earliest improvement in forest trees, such as poplars, for which economically feasible methods for clonal propagation of commercial planting stock are, or become, available.

For forest trees, as for agricultural crops (Harlan, 1966), it is the genus that through interspecific hybridization can provide the wide diversity of genotypes needed for maximum genetic improvement.

Interspecific and remote intraspecific breeding of poplars can easily provide a broad genetic base for the establishment of gene pools, and for the selection of ortets for clonal tests and continued breeding; relatively large numbers of seeds are obtainable by controlled pollination on flowering branches in water culture or bottle-grafted (Wettstein, 1930; Schreiner, 1959; Farmer and Nance, 1967). The western AIGEIROS poplars—*P. deltoides* var. *occidentalis*, *P. fremontii* and *P. fremontii* var. *wislizeni*—particularly outlier or fringe populations, may be extremely valuable for the introduction of important traits like drought and pest resistance.

But species hybridization in poplars should not be limited to intra-section crosses. Long-term tests in the United States and abroad of hybrids produced in 1925 and 1926 (Stout and Schreiner, 1933) have demonstrated that hybrids between AIGEIROS and TACAMAHACA poplars can be of particular value for increased growth rate, wider environmental adaptability, increased pest resistance, and improved timber and wood qualities.[3]

Fortunately, the possibilities for successful distant hybridization are particularly favorable in *Populus*, although there is evidence of lack of crossability between at least some individuals of different poplar species; for example the frequent failure of *P. nigra* (♀) x *P. deltodies* (♂) in contast to the reciprocal *P. deltoides* (♀) x *P. nigra* (♂) cross (Melchoir and Seitz, 1968). Where barriers between species are encountered it may be possible to obtain the desired combination by such methods as the use of irradiated mentor pollen (Stettler, 1968), through bridging crosses (Burnham, 1966), autotriploidy (Moav, 1962), or embryo culture.

Because clonal propagation permits the immediate multiplication and use of genetically superior individuals *without dilution or adulteration of the genotype*, earliest and maximum improvement will require the creation of synthetic multiclonal hybrid varieties. When individual clones in a multiclonal variety begin to lose their value because of a change in industrial use requirements, increasing disease or insect susceptibility, or decline of general fitness resulting from long-term climatic changes, they could be replaced by new clones selected from appropriate regional clonal tests.

Variance associated with cloning, the "c" effects (Libby and Jund, 1962), topophysis, cyclophysis, and periphysis (Klaehn, 1963), has been demonstrated. Libby and Jund have observed:

> Where appreciable 'c' effects associated with cloning exist, bias and overestimates of broad-sense heritability and the total genetic and non-additive genetic components of variance will result if some forms of clonal analysis are used. In addition, such effects will also reduce the efficiency of selection based on the performance of clones. The clonal component of variance for characters which are scored soon after cloning, such as four-week height, is likely to contain a high level of 'c' effects variance. However, characters which develop later probably contain a lower or vanishing level of 'c' effects in the clonal component. Internal physiological balances and

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[3] Bugala, 1959; Bugala and Stecki, 1961; Donaubauer, 1966; Eschner, 1960; Fröhlich, 1966; Funk, 1963; Guldemond, 1966; Günzl, 1967; Kerestesi, 1968; Pohl, 1962; Schlenker, 1964; Sebald, 1959; Shipman and Baldwin, 1966; Werner and Dagenbach, 1965; Zycha and Fröhlich, 1966.

> systems within each ramet will have developed in response to the unique micro-environments of the different ramets, largely replacing the common physiological and morphological condition of the vegetative parts at the time of cloning. This trend toward autonomy is clear in Donald's experiment with cattle twins, and in the four *Mimulus* experiments described above.

The occurrence of the variance associated with cloning must be recognized and considered in any improvement program with plants that are to be utilized as clones. But the ancient use of clones in horticulture, agriculture, and particularly in poplar culture, is ample evidence that the variance will be of little, if any, importance in the commercial culture of selected poplar clones.

Breeding Methods

Breeding to obtain multiclonal hybrid varieties should follow the same general methods as for the development of synthetic varieties to be propagated by seed, including intraspecific pedigree breeding (particularly remote intraspecific crosses), species hybridization, controlled sib- and back-crosses, and some kind of recurrent selection (Schnell, 1961; Borlaug, 1966).

Polyploidy will have particular value for the production of fast-growing poplars; there is considerable work in many countries on this aspect. Schlösser (1967) has produced progenies of tetraploid hybrids by controlled pollinations between the female clones 'Oxford' and 'Rochester' and the male clone 'Androscoggin' (Schreiner and Stout, 1934). The tetraploid populations exhibited a wide range of variation in early growth rate and particularly in resistance to *Melampsora* rust. The parent hybrids were only slightly susceptible (class 1 on a scale from 0 to 5) when grown at Hann.-Münden where there is always a high degree of natural rust infection; the tetraploid population varied from class 0 to 4. These tetraploids will be selected for use in further breeding to produce triploids with a rapid growth rate and the assurance of high disease resistance.

The use of monoploid breeding and also of androgenesis (Chase, 1951, 1963) should not be overlooked. The role of haploids (monoploids) in tree improvement and forest genetics has been reviewed by Kopecky (1960), Nei (1963), and Stettler (1966).

Mutagenesis is another approach that could be used, particularly to enhance the possibilities for increased disease resistance, and for diversification of genetic variability beyond that attainable from the reservoir of cryptic variability available in natural populations.

The number ($2x = 38$) and particularly the small size of poplar chromosomes have hindered essential basic cytological studies. Peto (1938), van Dillewijn (1940), and Smith (1943) have laid the foundation; much more work is required.

The need for basic studies on heritability should always be considered in breeding and progeny testing. The genetic improvement of clones selected for commercial use from properly designed and adequately "time-tested"[4] clonal field trials may be estimated directly from the clonal means. However, heritability in the narrow sense will be very useful if the clones are to be used for breeding.

Plus-tree Selection

The essential first step for the genetic improvement of *P. deltoides* should be the selection of plus trees from all regions of its natural range for clonal tests and for the establishment of gene pools. A 5-year goal might be a minimum of approximately 500 plus trees, including 200 trees from the region in which the work is undertaken, and 10 trees from each of 30 widely separated localities within the natural range of the species.

The selection of plus trees for most traits should be limited to individuals between 10 and 25 years of age. With few exceptions (such as selection for pest resistance) it will be advisable to eliminate trees that are remnants of old stands because it is very seldom possible to evaluate the early environmental conditions to which such trees were exposed.

Plus-tree selection should be based on both forest requirements and use requirements. Because *perfect* trees with all of the desired forest and use requirements will be extremely rare, it will be advisable to set up certain selection objectives in special categories for which minimum requirements for other traits, including growth rate, are not made too restrictive. This would apply particularly to selection for pest resistance, site adaptability, and special wood characteristics.

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[4] Beware of the "eager-beaver fever"; the urge to recommend clones for commercial planting on the basis of juvenile or even sapling evaluation. Long personal experience has demonstrated that about 90 percent of the hybrid clones selected on the basis of 4-year nursery performance have failed in 15-year tests. Smith and Blom (1966) have also stressed the ". . . need for long-term research to reduce risks."

Pest resistance is particularly important for the improvement of poplars; therefore, selection for apparent resistance to any pest, whether or not it is now a serious menace to poplar culture, is justified for *future improvement breeding.* Selection for resistance to a particular pest may have to be for this character alone. Inferior growth rate should not disqualify a tree except in cases where some aspect of growth rate is known or suspected to affect resistance.

All plus trees should be treated in the following manner. Several large branches in the top should be cut back (pollarded) during the dormant season for the production of sprout growth to be used as cutting stock. Sufficient crown should be left for the production of flowers and seed. Cooperation on a range-wide basis will be required for the selection and pollarding of plus trees and for the exchange of cutting stock, flowering branches, seed, control-pollinated stock, and tested clones.

When 100 plus trees are available, genetic improvement may begin on any one, on any combination, or on all of the four procedures outlined in figure 4: (I) plus tree clonal propagation; (II) half-sib propagation; (III) intraspecific breeding; and (IV) species hybridization.

Clonal Field Tests

The evaluation of clones for use in synthetic multiclonal varieties will require field tests of adequate design. Although initially selected for phenotypic superiority, these clonal tests (PT–C, HS–C, IB–C, SH–C, in fig. 4) can serve also as gene pools for pedigree breeding and mass selection.

The number of field tests required in any region will depend upon the variation in planting sites on which the poplars are to be grown; the clonal tests should sample the range of the expected commercial planting sites. Planting stock, site preparation, and subsequent cultural treatments applied to the clonal tests should be the same as those anticipated for commercial plantations. Pest-control measures that are considered economically feasible should be applied to only a part of each clonal test to permit evaluation of resistance among the untreated ramets.

I suggest two minimum, alternative, field designs for the clonal tests indicated under procedures I to IV (fig. 4).

1. A completely randomized planting of 10–20 ramets per clone at 12 feet x 12 feet spacing[5] on each test site. This would accommodate 30 clones per acre with 10 ramets per clone, or 15 clones per acre with 20 ramets per clone.
2. Five replicates of 4-tree clonal row-plots on each test site with ramets spaced 6 feet apart in the rows and the rows spaced 12 feet apart. This will permit thinning (within clones) to an approximate 12 feet x 12 feet spacing and will accommodate 30 clones per acre per site.

The clonal field tests should be evaluated periodically; the 4-tree rows may be thinned within clones, but clonal tests should not be rogued if they are to be maintained as gene pools. When clones are rated inferior for the combination of traits required for commercial planting they should be eliminated from further use if they were originally included in synthetic multiclonal varieties. On the basis of long personal experience I most strongly recommend that the selection of new clones for commercial use be delayed to at least half rotation age.[6] Such clones, and clones superior in single traits, may also be used for pedigree breeding or mass selection when they begin to flower.

Open-pollinated seed should be collected during 2 or more years when practically all trees in the plantation have reached full flowering age. This seed will provide seedlings for nursery evaluation and selection of ortets for the establishment of second-cycle clonal tests and gene pools.

The cost of establishment, culture, and maintenance of clonal test plantations may be partially or completely amortized (as in Europe) by clearcutting at 30 to 35 years. This length of the test period is suggested to provide sufficient time for adequate evaluation of pest resistance and environmental adaptability.

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[5] This spacing is based on the McKnight and Biesterfeldt (1968) report that in current commercial plantations in the south, cottonwoods are planted about 10 feet apart and that an intensive study at the Southern Hardwoods Laboratory indicates that 12 feet x 12 feet spacing is probably optimum for most products.

[6] Half-rotation age may vary from 4 to 15 years, depending upon the product objective, the intensity of commercial culture, and the natural environmental growth potential.

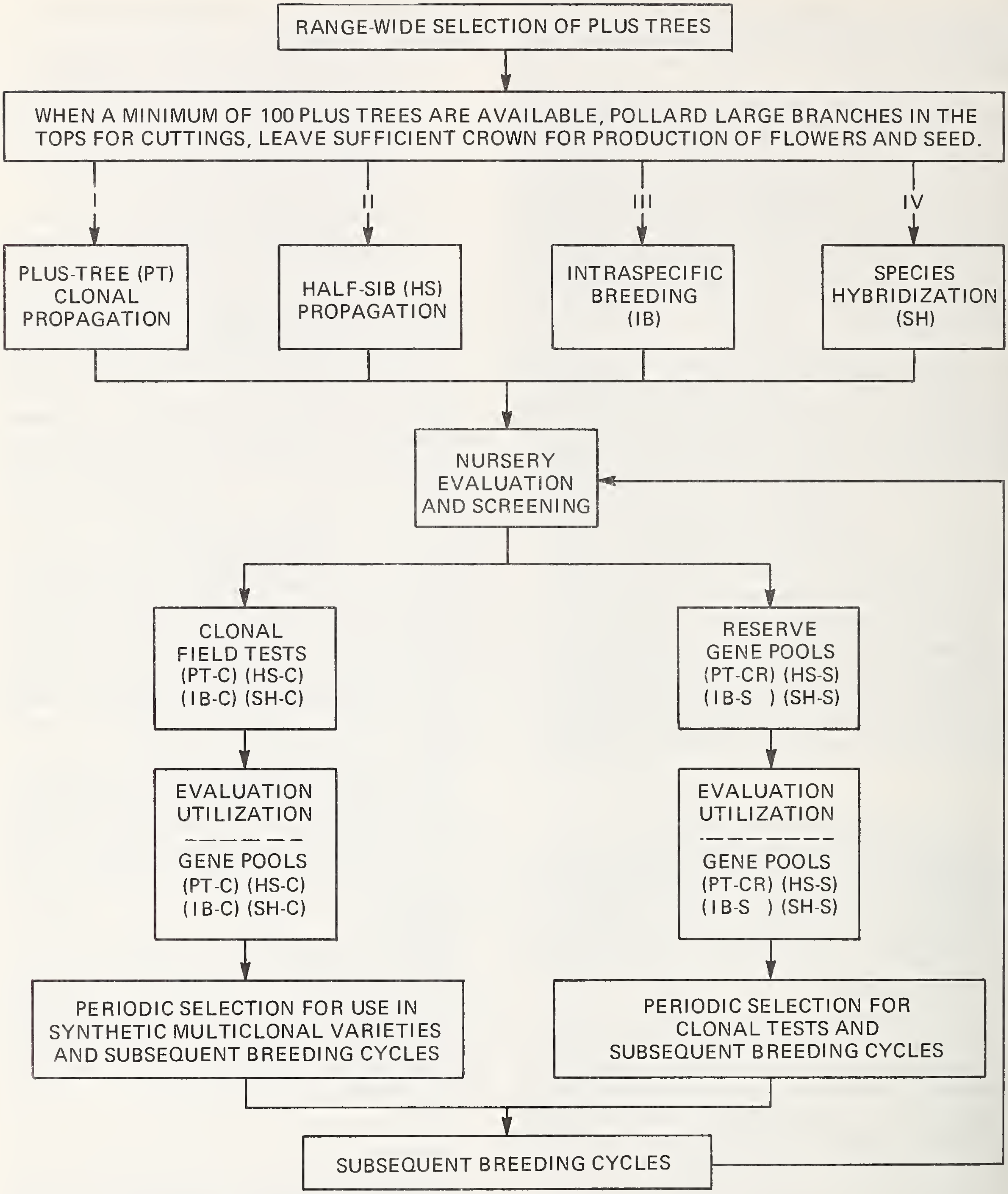
RANGE-WIDE SELECTION OF PLUS TREES
WHEN A MINIMUM OF 100 PLUS TREES ARE AVAILABLE, POLLARD LARGE BRANCHES IN THE TOPS FOR CUTTINGS, LEAVE SUFFICIENT CROWN FOR PRODUCTION OF FLOWERS AND SEED.
I
II
III
IV
PLUS-TREE (PT) CLONAL PROPAGATION
HALF-SIB (HS) PROPAGATION
INTRASPECIFIC BREEDING (IB)
SPECIES HYBRIDIZATION (SH)
NURSERY EVALUATION AND SCREENING
CLONAL FIELD TESTS (PT-C) (HS-C) (IB-C) (SH-C)
RESERVE GENE POOLS (PT-CR) (HS-S) (IB-S) (SH-S)
EVALUATION UTILIZATION
GENE POOLS (PT-C) (HS-C) (IB-C) (SH-C)
EVALUATION UTILIZATION
GENE POOLS (PT-CR) (HS-S) (IB-S) (SH-S)
PERIODIC SELECTION FOR USE IN SYNTHETIC MULTICLONAL VARIETIES AND SUBSEQUENT BREEDING CYCLES
PERIODIC SELECTION FOR CLONAL TESTS AND SUBSEQUENT BREEDING CYCLES
SUBSEQUENT BREEDING CYCLES

Figure 4.—Procedure for maximum genetic improvement of *Populus deltoides*.

Gene Pools

Gene pools of *both native and exotic* poplar species should be established at all centers of poplar improvement to provide the broadest possible genetic base, on the sound assumption that many of the future needs for genetic improvement are not known at present. This objective requires the conservation of both identifiable and cryptic variation. Therefore it is necessary to recognize the distinction between the sampling and the preservation of variability and the sampling and preservation of superiority: to collect and preserve the fullest possible genetic diversity rather than limit collection and preservation to preconceived ideas of superior phenotypes (Schreiner, 1968). Ideally, gene pools of both native and exotic species should be established with randomly selected seedlings derived from randomly selected parents. Such random sampling of *P. deltoides* would materially, and perhaps unnecessarily, enlarge the improvement program.

Procedure II (half-sib propagation, fig. 4) involves the selection of parents for phenotypic superiority. Nevertheless, if 10 plus trees from each locality throughout the range of the species are selected from different stands to avoid close relationship, the half-sib seedlings could be expected to provide a wide range of variation. Procedure III may be expected to provide additional genetic variability, and procedure IV will provide the wide genetic diversity resulting from species hybridization.

In contrast to seed orchards, gene pools should not be isolated to preserve their genetic integrity. For maximum future usefulness, forest tree gene pools should be designed for maximum panmixis to permit extensive recombination of genes through free pollination (Schreiner, 1968). Such mass intra- and interspecific hybridization can provide a practically inexhaustible source of gene combinations for the creation of synthetic clonal varieties over a long span of years; this could save many years of controlled breeding.

Within a region, gene pool plantations should sample a reasonable range of the predictable commercial planting sites. A minimum field design for seedling gene pools (HS–S, IB–S and SH–S, fig. 4) could be a completey randomized planting, on each gene-pool site, of 10 to 20 seedlings per progeny at a *minimum* spacing of 10 feet x 10 feet.[7] This would accommodate 43 or 21 progenies per acre with 10 or 20 seedlings per progeny, respectively. Complete randomization will increase the chance for free crossbreeding between seedlings of the different progenies. A minimum field design for the reserve clonal gene pools (PT–CR, fig. 4) would be a completely randomized planting of 5 to 10 ramets per clone spaced 10 feet x 10 feet (86 to 43 clones per acre per site). Seedling gene pools and reserve clonal gene pools established in the same year may be combined to considerable advantage.

To maintain maximum genetic diversity, the gene pools should not be rogued or thinned. Seedlings and clones should be rated not only on the *combination* of superior characteristics desired for commercial planting but also on the basis of special characteristics such as superior growth rate, pest resistance, excellent timber form, and particular wood properties. Beginning at half-rotation age, ortets of superior promise for commercial use may be selected and multiplied for clonal tests; those with superior individual traits may be used for subsequent pedigree breeding or mass selection when they come into bloom. Such selections from both the gene pools and the clonal field tests will represent a decreasing calculated risk until end of rotation.

The extensive natural range of *P. deltoides* and the evidence for ecotypic variation in the photoperiodic response indicates the need for range-wide provenance tests, but this would unnecessarily increase the improvement program. The half-sib gene pools can provide the provenance information needed for practical improvement selection and breeding.

Gene-pool plantations may be liquidated at 30 to 35 years; open-pollinated seed should be collected during at least 2 years of peak flowering for the establishment of second-cycle gene-pools and clonal tests.

Plus-tree Clonal Propagation and Evaluation

Selection and clonal testing of plus trees is the simplest improvement procedure and can begin to provide material for commercial planting within 3 to 4 years. There would be relatively little risk in using 25 to 50 local plus-tree clones in *synthetic multiclonal varieties* before field tests have indicated the superior clones, and the increased risk in using some selections from other regions in such multiclonal varieties would be slight.

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[7] The spacing in gene pools should be increased to at least 12 feet x 12 feet if the land area is available. See footnote 5.

Nursery propagation and screening.—At least 25 cuttings from sprout growth on the pollarded branches of each plus-tree ortet should be propagated in a replicated nursery stool-planting during the first year. This would constitute a preliminary rooting test and a preliminary screening for diseases and insects that may occur naturally in the nursery. A second replicated stool-planting for final rooting tests and nursery screening should be established in the second year with a minimum of 50 graded cuttings from the first-year stools of each clone. Poor-rooting and pest-susceptible clones *that were not selected for special traits* should be discarded at the end of the second year.

Clonal field tests (*PT–C*).—Field tests of the clones selected for good rooting and satisfactory nursery screening for other characteristics such as growth rate and pest resistance could begin in the third or fourth year with cuttings or in the fourth or fifth year with 1-year-old rooted cuttings. Minimum acceptable rooting under good nursery conditions should not be less than 95 percent or 75 percent depending on whether cuttings or nursery-rooted trees, respectively, are to be used for commercial outplanting.

Reserve plus-tree gene pools (*PT–CR*).—Clones not selected for clonal field tests, including poor-rooting and pest-susceptible clones of plus trees *that were selected for special traits,* should be preserved in one or more reserve gene pools.

Clones for use in synthetic multiclonal varieties.—Stools of clones selected for clonal field tests will constitute a source of cuttings for commercial use in synthetic multiclonal varieties on the basis of a calculated risk. All other stools may be removed from both the first- and second-year nursery plantings.

Half-sib Propagation

Nursery propagation and screening.—The dual objectives for half-sib propagation and evaluation would be: (1) clonal field tests of ortets selected on the basis of nursery screening; and (2) establishment of combination "gene pool-progeny test" plantations, primarily to provide gene pools for future clonal selection and breeding, but also to obtain some information on heritability.

On the basis of 500 plus-tree selections over a 5-year period, it is a safe assumption that not more than 250 will be female trees. A reasonable program might entail propagation and nursery evaluation of a minimum of 200 half-sibs from each of approximately 50 plus trees each year. Selection of ortets for replicated nursery rooting tests and screening probably could be made with 1-year-old seedlings grown in southern nurseries, but 2-year-old seedlings would be required from northern nurseries (unless seedlings are started under portable plastic greenhouses).

From personal experience with 15- to 20-year clonal tests of full-sib hybrid ortets selected at 2 and at 15 years of age, I would recommend, if possible, the selection of 20 half-sibs (on the basis of individual growth-rate, resistance to nursery pests, and any other important juvenile characteristics) of each of the 1- or 2-year-old progenies in the upper 50 percent in average height growth for final tests of rooting ability and nursery screening.[8]

Clonal field tests (*HS–C*).—The intensity of selection for clonal field tests, to be begun with cuttings at the end of the third or fourth years or with 1-year-old rooted cuttings at the end of the fourth or fifth years, must depend on the facilities available for establishment and maintenance of the plantations.

Seedling gene pool-progeny test plantations (*HS–S*).—As many progenies as possible should be represented in the gene pool-progeny test plantations to be established with the 1- or 2-year-old seedlings. Because the objective is to provide a broad genetic base for future clonal selection and breeding, and to obtain some measure of heritability, the seedlings for these plantations should represent a random sample of each progeny. Therefore, they should be randomly selected *before* the best individuals in the best progenies are selected for clonal tests. Inherently superior individuals included in the gene pools will be available for future selection for clonal tests and breeding.

Intraspecific Breeding

Controlled intraspecific breeding may begin in the same year as plus-tree and half-sib propagation, but there would be some advantage in delaying controlled breeding until preliminary information is available from the nursery evaluation of plus-tree ramets and half-sib progenies. Although the value of 2-year nursery data is questionable as a measure of inherent potentialities, it may be used to some advantage in selecting parents to be used for controlled intraspecific breeding, particularly with reference to nursery pest resistance.

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[8] In a 2-year test of half-sib cottonwood families, Farmer and Wilcox (1966b) found wide variation in narrow-sense heritabilities for first and second year height and diameter growth. They point out that the lack of data on juvenile-mature correlations suggests the need for extensive selection in nursery tests. They conclude, "Thus, in our material, clonal testing of the top 10 percent of phenotypes in the top 20 percent of families would appear to be a safe and productive procedure at this stage of breeding."

Individual crosses between 500 plus trees (62,500 crosses, assuming 250 trees of each sex) would be beyond the scope of any regional breeding project and will not be necessary. The primary objective of intraspecific breeding in poplars should be the production of genetically superior individuals for use in synthetic clonal varieties, and the release of cryptic variability through recombinations on as large a scale as possible. This may be accomplished by the use of pollen mixtures of five or more plus trees from different stands (to avoid close relatives) in each of several geographic regions within the natural range of the species for the pollination of female plus trees from various provenances.

As a minimum program, intraspecific hybridization in any one year might be limited to the use of pollen mixtures from plus trees in five geographic regions on 10 females, five from the same provenances as the males, and five from the local region. With complete success, this would provide a maximum of 50 progenies. Breeding and nursery propagation should aim at a minimum of approximately 200 seedlings per progeny.

The clonal field tests (IB–C) and seedling gene pools (IB–S) can be established, evaluated, and utilized as previously described.

Species Hybridization

Species hybridization will provide the maximum genetic diversity in both forest and use requirements essential for the development of synthetic multiclonal hybrid varieties adapted to a wide range of environmental conditions. Hybridization with *P. deltoides* can begin as soon as pollen and female flowering branches are available, or it can be delayed until nursery evaluation has provided at least very preliminary information on nursery performance of the plus trees and on the general combining ability of the female plus trees included in the half-sib tests.

All available poplar species should be used as both male and female parents; this will require national and international cooperation for the exchange of pollen and flowering branches. Within-provenance pollen mixtures from different provenances of native and exotic species, and pollen of plus trees and superior hybrids in commercial use should be used for hybridization with *P. deltoides.*

Hybrids between many species (both within and between sections) are so easily produced that the number of seedlings per progeny will have to be limited. Species hybridization and nursery propagation should aim at a minimum of approximately 200 seedlings per progeny. It is conceivable that projects in different regions will eventually concentrate on the large-scale production of species hybrids that have shown most promise in the region.

The clonal field tests (SH–C) and seedling gene pools (SH–S) can be established, evaluated, and utilized as previously described. The clonal field tests should include superior clones of *P. deltoides* as standards for rating the hybrid clones. Seedling progenies and superior clones of *P. deltoides* from several provenances and other species, varieties, and clones used as parents for hybridization, should be included in the hybrid gene pools.

LITERATURE CITED

Arru, Giovanni M.

1964–65. *Pygaera anastomosis* (L.) (Lepidoptera Notodontidae) Studio morfologico ed etologico. Boll. di Zoologia agraria e di Bachicoltura, Serie II, 6: 207–271.

Arru, Giovanni M.

1966–67. I piu importanti Insetti minatori delle foglie di pioppo nell'Italia settentrionale. Boll. di Zoologia agraria e di Bachicoltura, Serie II, 8: 41–74.

Avanzo, E.

1967. Investigation biometrique sur les bougeons a fleurs d'un individu bissexue de *Populus deltoides* Marsh. XIV IUFRO-Congress 3: 72–76. Munich.

Barner, J.

1965. Experimentelle Untersuchungen über das Verhalten von Forstpflanzen gegenüber Licht and Schatten als Grundlagenerhebung für die Standorts- und Rassenwahl. Mitt. Ver. f. Forst. Standortskunde und Forstpflanzenzüchtung Nr. 15: 65–69.

Borlaug, Norman E.
1966. Basic concepts which influence the choice of methods for use in breeding for disease resistance in cross-pollinated and self-pollinated crop plants. *In* Breeding Pest-Resistant Trees. p. 327–344. London: Pergamon Press.

Boyce, Stephen G., and Kaeiser, Margaret.
1961. Environmental and genetic variability in the length of fibers of eastern cottonwood. Tappi 44(5):363–366.

Brayshaw, T. C.
1966. Native poplars of southern Alberta and their hybrids. Canada Dep. of Forest, Publ. 1109. 40 p.

Broadfoot, W. M., and Bonner, F. T.
1966. Soil compaction slows early growth of planted cottonwood. Tree Planters' Notes 79: 13–14

Bugala, Wladyslaw.
1959. Kolekcja topoli w Arboretum Kornickim. Arboretum Kornickie, Rocznik 4: 123–164.

Bugala, Wladyslaw, and Stecki, Zbigniew.
1961. Mieszance *Populus maximowiczii* Henry i dotychczasowe wyniki ich uprawy w Korniku. Arboretum Kornickie, Rocznik 6: 93–116.

Burnham, C. R.
1966. Cytogenetics in plant improvement. *In* Plant Breeding. p. 139–187. Ames, Iowa: Iowa State Univ. Press.

Cadahia, D.
1965. Preferencias clonales del gorgojo perforado del chopo *Cryptorrhynchus lapathi* L. (*Col. Curculionidae*). Boletin del Servicio de Plagas Forestales 8(16): 115–125.

Chase, Sherret S.
1951. The monoploid method of developing inbred lines. Proc. 6th Annual Hybrid Corn Industry—Research Conf., Nov. 28–29, 1951. Chicago. 5 p.

Chase, Sherret S.
1963. Androgenesis—its use for transfer of maize cytoplasm. J. Hered. 54(4): 152–158.

Chiba, Shigeru.
1966. Studies on tree improvement by means of artificial hybridization and polyploidy in *Alnus* and *Populus* species. Bull. Oji Inst. for Forest Tree Impr. No. 1. 165 p. Kuriyama, Hokkaido, Japan.

Craighead, F. C.
1950. Insect enemies of eastern forests. U.S. Dep. Agr. Misc. Publ. 657. 679 p.

Curlin, James W.
1967. Clonal differences in yield response of *Populus deltoides* to nitrogen fertilization. Soil Sci. Soc. of Amer. Proc. 31(2): 276–279.

Dillewijn, C. van.
1940. Zytologische Studien in der Gattung *Populus* L. Genetica 22: 131–182.

Donaubauer, Edwin.
1966. On the resistance of various poplar clones to *Dothichiza populea* Sacc. et Br., *Septotinia populiperda* Watt. et Cash, and *Melampsora allii populina* Kleb. *In* Breeding Pest-Resistant Trees. p. 271–277. London: Pergamon Press.

Eschner, Arthur R.
1960. Observations on a hybrid poplar test planting in West Virginia. Northeast. Forest. Exp. Sta. Forest Res. Note 111. 4 p.

Farmer, Robert E., Jr.
1964. Sex ratio and sex-related characteristics in eastern cottonwood. Silvae Genetica 13(4): 116–118.

Farmer, Robert E., Jr.
1966a. Variation in time of flowering and seed dispersal of eastern cottonwood in the lower Mississippi Valley. Forest Sci. 12(3): 343–347.

Farmer, Robert E., Jr.
1966b. Cottonwood improvement in the lower Mississippi Valley. Southern Conf. on Forest Tree Impr. Proc. 8: 49–52.

Farmer, R. E., Jr., and Nance, W. L.
1967. Crossing eastern cottonwood in the greenhouse. Int. Plant Propagators Soc. Comm. Proc. 17: 333–338.

Farmer, R. E., Jr., and Wilcox, J.R.
1966a. Specific gravity variation in a lower Mississippi Valley cottonwood population. Tappi 49(5): 210–211.

Farmer, R. E., Jr., and Wilcox, J. R.
1966b. Variation in juvenile growth and wood properties in half-sib cottonwood families. Joint Proc. 2d Genetics Workshop Soc. of Amer. Foresters and 7th Lake States Forest Tree Impr. Conf. USDA Forest Serv. Lake States Forest Exp. Sta. Res. Paper NC–6: 1–4.

Food and Agriculture Organization of the United Nations.
1958. Poplars in forestry and land use. FAO Forestry and Forest Products Studies No. 12. Rome. 511 p.

Fowells, H. A.
1965. Silvics of forest trees of the United States. U.S. Dep. Agr. Hand. 271. 762 p.

Fröhlich, H. J.
1966. Pappelzüchtung und -andau. Der Forst- und Holzwirt 21 (12) : 1–5.

Funk, David T.
1963. Hybrid poplars on Ohio spoil banks. USDA Forest Serv. Res. Note CS-8.4 p. Central States Forest Exp. Sta.

Guldemond, J. L.
1966. De balsemkruisingen *Populus* 'Androscoggin', *Populus* 'Geneva' en *Populus* 'Oxford'. Bosbouwproefstation "DeDorschKamp" Bericht 53: 8p.

Günzl, Leopold.
1967. Anbauergebnisse and Erfahrungen mit Pappelhybriden. Centralblatt f. d. Gesamte Forstwesen 84(1) : 21–35.

Hamilton, J. R., and Wendel, G.W.
1967. Specific gravity and fiber length of some hybrid poplars growing in West Virginia. W. Va. Univ. Agr. Exp. Sta. Bull. 556T, 6 p.

Harlan, J.R.
1966. Plant introduction and biosystematics. *In* Plant Breeding. p. 55–83. Ames, Iowa: Iowa State Univ. Press.

Henry, Augustine.
1914. The artificial production of vigorous trees. J. Dep. Agr. and Tech. Inst., Irish Fee State. 15: 34–52.

Kennedy, R. W.
1957. Fibre length of fast- and slow-grown black cottonwood. Forestry Chron. 33(1) : 46–50.

Kerestesi, Bela.
1968. Forest tree improvement in Hungary. Unasylva 22(1) : 14–17.

Klaehn, Friedrich Ulrich.
1963. The relation of vegetative propagation to topophysis, cyclophysis, and periphysis in forest trees. NE. Forest Tree Impr. Conf. Proc. 10(1962) : 42–50.

Kopecky, Ferenc.
1960. Experimentelle Erzeugung von haploiden Weisspappeln (*Pouplus alba* L.). Silvae Genetica 9(4) : 102–105.

Lester, Donald T.
1963. Variation in sex expression in *Populus tremuloides* Michx. Silvae Genetica 12(5) : 141–151.

Libby, W. J., and Jund, E.
1962. Variance associated with cloning. Heredity 17: 533–540.

Maisenhelder, Louis C.
1960. Cottonwood plantations for southern bottom lands. South. Forest Exp. Sta. Occas. Pap. 179. 24 p.

Marton, Renata, Stairs, G. R. and Schreiner, E. J.
1968. Influence of growth rate and clonal effects on wood anatomy and pulping properties of hybrid poplars. Tappi 51(5) : 230–235.

McKnight, J. S., and Biesterfeldt, R. C.
1968. Commercial cottonwood planting in the southern United States. J. Forest. 66: 670–675.

Melchior, G. H.
1967. Zwei Funde von Zwittrigkeit an Pappeln der Sektion Aigeiros. Silvae Genetica 16(2) : 77–80.

Melchior, G. H., and Seitz, F. W.
1968. Interspezifische Kreuzungssterilität innerhalb der Pappelsektion Aigeiros. Silvae Genetica 17(2–3) : 88–93.

Moav, Rom.
1962. Inheritance in *Nicotiana tobacum.* XXX: Autotriploidy, a possible means of increasing the rate of interspecific gene transfer. Hered. 17: 373–379.

Nei, Masatoshi.
1963. The efficiency of haploid method of plant breeding, Hered, 18: 95–100.

Pauley, Scot S., and Perry, Thomas O.
1954. Ecotypic variation of the photoperiodic response in *Populus.* J. Arnold Arboretum 25: 167–188.

Peto, F. H.
1938. Cytology of poplar species and natural hybrids. Canad. J. Res. C 16: 445–455.

Pohl, Zygmunt.
1962. Studia nad wzrostem i morfologia kornickich mieszancow *Populus Maximowiczii* Henry. Arboretum Kornickie, Rocznik 7: 115–187.

Rehder, Alfred.
1940. Manual of cultivated trees and shrubs. 2d ed. 996 p. New York: The Macmillan Co.

Ruehle, John L.
1967. Distribution of plant-parasitic nematodes associated with forest trees of

the world. USDA Forest Serv. Southeast. Forest Exp. Sta. 156 p.

Sachsse, Hanno.
1961. Beitrag zur Kenntnis der Holzeigenschaften der Oxford-Pappel. Mitt. Ver. f. Forstl. Standortskunde and Forstpflanzenzüchtung, Stuttgart, No. 11 : 92–102.

Schlenker, G.
1964. Beobachtungen über das Jugendwachstum einiger Pappelsorten auf verschiedenen Standorten in Nordwürrtemberg. Der Forst—und Holzwirt 19 (12) : 1–5.

Schlosser, Ludwig-Arnold.
1967. Über den Rostbefall einer Population tetraploider Pappeln. Der Züchter 37: 298–300.

Schnell, F. W.
1961. On some aspects of reciprocal recurrent selection. Euphytica 10 : 24–30.

Schreiner, Ernst J.
1935. Possibilities of improving pulping characteristics of pulpwoods by controlled hybridization of forest trees. Paper Trade J. Tech. Sect. C 100 (8) : 105–109.

Schreiner, Ernst J.
1937. Silvicultural methods for reforestation with hybrid poplars. The Paper Industry. May: 156–163.

Schreiner, Ernst J.
1945. How sod affects establishment of hybrid poplar plantations. J. Forest. 43: 412–426.

Schreiner, Ernst J.
1949. Poplars can be bred to order. *In* U.S. Dep. Agr. Yearb. 153–157.

Schreiner, Ernst J.
1950. Genetics in relation to forestry. J. Forest. 48: 33–38.

Schreiner, Ernst J.
1958. Possibilities for genetic improvement in the utilization potentials of forest trees. Silvae Genetica 7 : 122–128.

Schreiner, Ernst J.
1959. Production of poplar timber in Europe and its significance and application in the United States. U.S. Dep. Agr. Handb. 150. 124 p.

Schreiner, Ernst J.
1960. Objectives of pest-resistance improvement in forest trees and their possible attainment. Proceedings of Fifth World Forestry Congress 2: 721–727. Seattle, Wash.

Schreiner, Ernst J.
1963. Improvement of disease resistance in *Populus*. Proceedings of World Consultation on Forest Genetics and Tree Improvement, Stockholm, FAO/FORGEN–63, vol. II, 6a/2 : 1–31.

Schreiner, Ernst J.
1966a. Future needs for maximum progress in genetic improvement of disease resistance in forest trees. *In* Breeding Pest-Resistant Trees. p. 455–466. London : Pergamon Press.

Schreiner, Ernst J.
1966b. Maximum genetic improvement of forest trees through synthetic multiclonal hybrid varieties. Northeast. Forest Tree Impr. Conf. Proc. 13 (1965) : 7–13.

Schreiner, Ernst J.
1967. Physiological and biochemical research on asexual reproduction in forest trees: an essential approach to early maximum genetic improvement. XIV IUFRO-Congress 3: 224–247. Munich.

Schreiner, Ernst J.
1968. Forest tree breeding. Unasylva 22 (3) : 3–9.

Schreiner, Ernst J., and Stout, A. B.
1934. Description of ten new hybrid poplars. Torrey Bot. Club Bull. 61: 449–460.

Sebald, O.
1959. Ergebnisse von Pappelsorten-Vergleichsversuchen. Mitt. Ver. f. Forst. Standortskunde und Forstpflanzenzüchtung No. 8: 3–34.

Shipman, R. D., and Baldwin, R. C.
1966. Planted hybrid poplar cuttings show variable resistance to drought. Tree Planters' Notes 79 : 23–28.

Smith, E. Chalmers.
1943. A study of cytology and speciation in the genus *Populus* L. Arnold Arboretum J. 24 : 275–305.

Smith, J. H. G., and Blom, G.
1966. Decade of intensive cultivation of poplars in British Columbia shows need for long-term research to reduce risks. Forestry Chron. 42 (4) : 359–376.

Stettler, Reinhard F.
1966. The potential role of haploid sporophytes in forest genetics research. Sexto Congreso Forestal Mundial, Madrid, June 1966, 6CFM/E/C.I.I/21. 7p.

Stettler, Reinhard F.
1968. Irradiated mentor pollen: its use in remote hybridization of black cottonwood. Nature 219(5155): 746–747.

Stout, A. B., McKee, R. H. and Schreiner, E. J.
1927. The breeding of forest trees for pulpwood. Jour. N.Y. Bot. Garden 28: 49–63.

Stout, A. B., and Schreiner, E. G.
1933. Results of a project in hybridizing poplars. J. Hered. 24: 216–229.

Vaartaja, O.
1960. Ecotypic variation of photoperiodic response in trees especially in two *Populus* species. Forest Sci. 6: 200–206.

Werner, H., and Dagenbach, H.
1965. Erfahrungen mit der Rochester-Pappel in schattigen Bachtälchen. Mitt. Ver. f. Forstl. Standortskunde und Forstpflanzenzüchtung Nr. 15: 56–64.

Wettstein-Westersheim, Wolfgang von.
1930. Die Züchtung von Pappeln (*Populus*). Der Züchter 2(7): 219–220.

Williamson, A. W.
1913. Cottonwood in the Mississippi Valley, U.S. Dep. Agr. Bull. 24, 62 p.

Zycha, H., and Fröhlich, H. J.
1966. Das Auftreten der Marssonina-Krankheit an Pappelarten und -sorten in der Bundesrepublik im Jahre 1965. Die Holzzucht Nr. 1/2: 1–8.

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1970. Genetics of eastern cottonwood. USDA Forest Serv. Res. Pap. WO-11, 24 p.

The eastern cottonwood (*P. deltoides*) is discussed as the basic species for the development of improved synthetic multiclonal varieties. All crossable species of *Populus* should be used for ultimate maximum genetic improvement of this genus. Major objectives of genetic improvement should be to obtain maximum production of wood for specific uses, wide environmental adaptability, and pest resistance. Procedures are suggested for early and maximum improvement through plus-tree selection, half-sib selection, and controlled intraspecific and interspecific breeding.

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